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Reaching Out: Cortical Mechanisms of Dispatch Directed Action

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Recordings from monkey cortex have demonstrated a sophisticated neural mechanism for the complex transformational mapping demanded by visually guided reaching.

Virtually everything we do can be thought of as either reaching or grasping. Reaching implies directed motion, as in moving the hand towards a tempting cake. It demands continual and rapid adjustments of motor activity in the light of sensory information about the location of the target, and about the position and movement of the limb that is doing the reaching. Grasping, on the other hand, requires no computation of positions and velocities: once contact is made, what is required is extensive feedback from the fingers so that the force they exert can be precisely controlled, the cake neither slipping from one's grasp nor being messily squashed.

Of these two fundamental actions, grasping is on the whole the simpler. Those areas of skin used for manipulation are richly endowed with receptors specialised for all the different kinds of information that can assist in gripping and safely lifting: sensing contact and deformation, tension, the shearing forces created by the gripped load, and the vibrations induced by slippage. At the same time, receptors in the bodies and tendons of the muscles signal load and stretch and rate of change of stretch.

Thanks to the classic work of Rosen and Asanuma [1] we have a clear picture of how this wealth of feedback is used. It projects to the primary motor cortex, a region which in primates has direct access to the motor neurons of the spinal cord, and seems to control directed force. The sensory afferents that impinge on a pyramidal cell controlling a particular gripping muscle provide information specifically relevant to that muscle's action: from its own spindles and tendon organs, and most dramatically, from sensory receptors in just those areas of skin brought into contact by the resultant grip. Primary cortex, long regarded as rather high in the motor hierarchy, is actually somewhere near the bottom, carrying out a relatively straight-forward mechanism of feedback control that is only located in the brain rather than spinal cord because it has to *learn* the underlying patterns of connection, too subtle to be specified genetically. The parts of the body most represented in primary motor cortex are those most used for manipulation. In our own case, the hands and mouth predominate; in monkeys, the feet are more represented than ours; the pig is all snout [2,3].

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It is instructive to compare this situation with the control of another probing and grasping organ, the eye. Here too, there are two distinct levels of control: *where*, the control of eye movements in relation to the visual position of targets in the outside world; and *how*, the extraordinarily precise control of force that keeps our eyes relatively fixed as we grip a target with our eyes. If we put the underlying motor circuits for these two systems side-by side (Figure 1), the parallels are obvious. In particular, it is striking that what primary motor cortex does for the hand is performed for the eye by a relatively primitive area, a part of the reticular formation. There is a simple reason for this difference: whereas motor commands to the arm and hand must be altered all the time to make allowance for the different loads that may be encountered, in the case of the eye the load is essentially constant. So no feedback is needed, except in the long term to counteract the effects of aging, fatigue and disease.

When we consider the second fundamental phase of movement, reaching, the parallels are even more obvious; and both systems face the same, inevitable, problem: *frames of reference*. Visual information from the retina immediately tells the brain where a target is, relative to where we are looking. But the command to move the eye must be framed not in these eye co-ordinates, but in *head* co-ordinates: the degree of deviation of the eye in the orbit needed to fixate an object seen at a particular position on the fovea clearly depends on where the eye itself happens to be. Thus a kind of transformation of axes must occur somewhere in the oculomotor system, in fact almost certainly in the superior colliculus, which appears to be provided not only with a visual map (necessarily in retinal coordinates) but also with information about where the eye is pointing [4].

Turning to the control of the hand, things are even more complex. Not only has the position of a target to be specified relative to the body, so that retinal location, eye position and head position as well must all be known; but if the eye is not looking at the hand (Figure 2A), then the visual co-ordinates must be neurally shifted to convert them into hand co-ordinates. Again, this task appears too complex to be undertaken by anything except cortex, and a recent study by Richard Andersen and colleagues [5] has elucidated what seems to be a specific mechanism in monkey posterior parietal cortex for carrying out these transformations.

Monkeys were trained to fixate a visual target with their hand at a specified initial position; then a target was presented at a new position, to which the monkey moved its hand. Meanwhile, implanted electrodes recorded the activity of neurons in two main locations: in dorsal area 5 of posterior parietal cortex (a region associated with the co-ordination of visuospatial information and the control of reaching movements and saccades), and also in the nearby parietal reach region (PRR). Such units typically fire in response to the

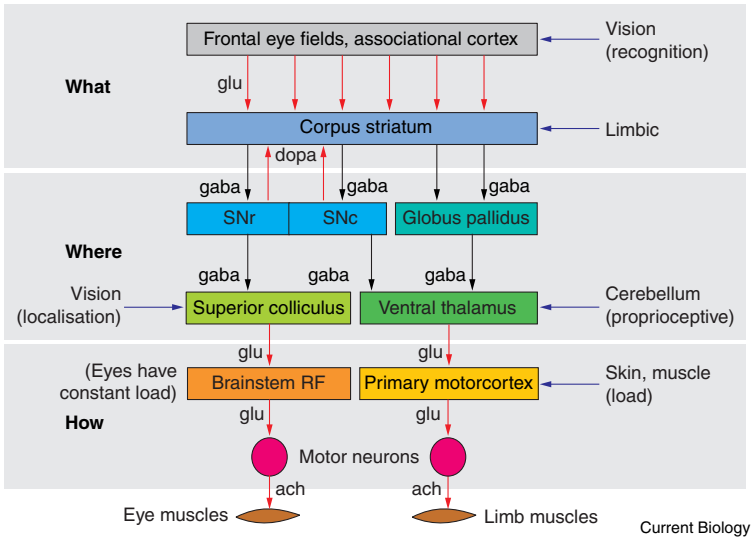

Figure 1. The fundamental motor hierarchy of deciding, reaching and grasping (what, where, how) for eye movements (left) and hand movements (right).

Each level is provided with the kind of sensory input it needs to carry out its computations. SNr, SNc: substantia nigra, pars reticulata and compacta; RF: reticular formation. Transmitters: dopa, dopamine; ach, acetylcholine; gaba, γ-amino butyric acid; glu, glutamate.

appearance of the target over a wide range of target positions, with the activity peaking at some particular, 'preferred' locus. Thus, the profile of activity of an ensemble of such units can provide a good representation of target position. By systematically varying the position of the target in terms of initial hand position and the point of fixation, the investigators were able to plot maps like the one shown in Figure 2B, showing the extent to which a particular neuron was 'thinking' in terms of hand co-ordinates or eye co-ordinates.

To interpret such maps, it is helpful to consider the various theoretical possibilities. If a neuron simply coded target position in relation to the eye, then the hand should not affect its response: we should get a vertically organised map like the one on the left of figure 2C. Another possibility is that the hand position modulates the activity, but does not shift the preferred retinal locus: this in fact was the kind of response seen in neurons from PRR, and is reminiscent of what has previously been described by the same group [6,7] in a parietal area concerned with implement -ing a head/eye transformation mentioned of the kind described earlier.

Finally, different positions of the hand could *shift* the peak of the distribution. This shift might be partial (third from the left, Figure 2C), or complete — in which case the unit would in effect be responding in hand co-ordinates rather than eye co-ordinates. The area 5 units do not in fact seem to go this far. As in Figure 2B, they show clear evidence of a partial shifting, a half-way house on the way to providing the hand-centred representation needed actually to control the muscles.

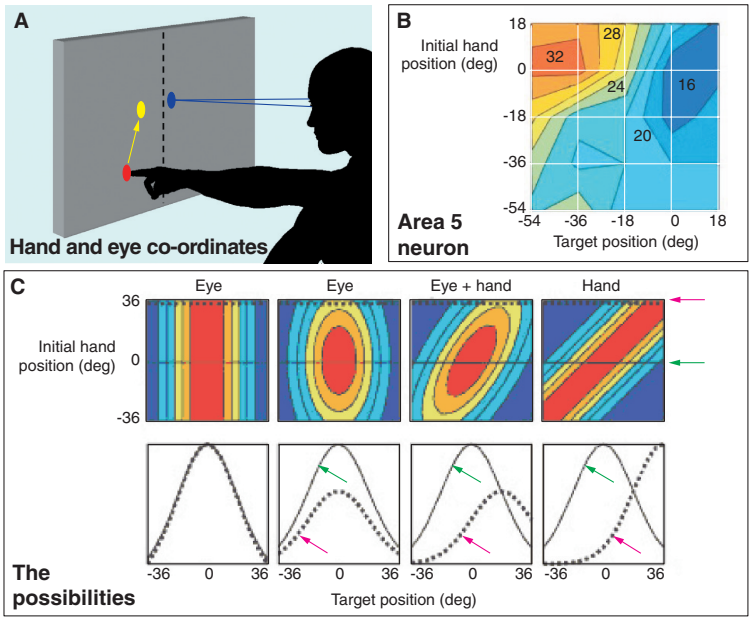

Figure 2.

(A) In some conditions, the position of a target (yellow dot) for a hand movement may be quite different relative to the initial position of the hand (red) and relative to where the eye is fixating (blue). (B) Firing of a neuron from monkey cortical area 5 as a function of horizontal target position relative to the eye (horizontal axis) and initial hand position (vertical axis). The firing frequency in Hz is shown on the map. (C) Some theoretical possibilities. From left to right they are: neuron responding in eye coordinates only; eye coordinates, but amplitude modulated by hand position; eye co-ordinates partly shifted and modulated by hand position; hand co-ordinates. The curves below show the profile of activity for an initial hand position of zero (green arrow), and of 36° (pink arrow). (Partly after [5].)

It is easy to see how this partial shifting could be achieved by combining the signals from a number of neurons whose maps are not shifted, but – like the neurons in PPR — simply modulated by hand position. As Andersen and colleagues [5] point out, the demonstration that the maps can be shifted at all means there is no reason why other regions of the brain, perhaps more directly concerned with muscular control, could not create wholly hand-centred maps.

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